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Oxidant Air Pollution Effects on a Western Coniferous Forest Ecosystem

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ENVIRONMENTAL RESEARCH BRIEF

Oxidant Air Pollution Effects on a Western Coniferous Forest Ecosystem

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Abstract

From 1973 to 1978, an interdisciplinary study of the pine and mixed conifer forests of the San Bernardino Mountains of southern California measured the effects of 30 years' exposure to photochemical oxidant air pollution on selected ecological systems. Average 24-hour ozone concentrations in the San Bernardino Mountains during the May through September period ranged from a background of 3-4 pphm up to a maxima of 10-12 pphm. Ponderosa pine was very ozone sensitive; foliar injury occurred at 24-hour concentrations of 5-6 pphm followed by, in decreasing order of sensitivity, Jeffrey pine, white fir, black oak, incense cedar, and sugar pine. Foliar injury and premature leaf fall caused decreased photosynthetic capacity, suppressed radial growth of stems (a negative exponential relationship), and reduced nutrient retention in the green biomass, all leading to weakened trees. Pines became more susceptible to root rot *(Fomes annosus)* and pine beetles *(Dendroctonus brevicomis);* mortality rates reached 2-3 percent in some years. Litter depth was greatest in stands receiving the most injury and associated defoliation, hindering pine seed establishment but encouraging oxidant-tolerant species in the understory. The living foliage of smaller trees, which can be easily ignited by ground fires in the understory combined with increased litter accumulation, fuels a more destructive type of fire. Fire and ozone destruction of the pine forest overstory leads to a dominance of self-perpetuating, fire-adapted, ozone-tolerant, shrub and oak species mixtures that provide fewer commodity and amenity values than the former pine forest. Change was evident in four ecosystem processes: the flows of water, carbon and nutrient and changes in patterns of diversity in time and space.

Introduction

The mixed conifer forests in the San Gabriel and San Bernardino mountain ranges east of Los Angeles have been exposed to oxidant air pollution since the early 1950's.[1] The symptoms of chronic ozone injury to sensitive tree species are visible up to 120 km east of urban centers in southern California and from 50 to 70 km east of central valley cities in parts of the Sierra Nevadas.[2,3] The extensive visible injury, and a concern for possible adverse effects on forest ecosystem stability under continuing exposure, led to an interdisciplinary study on the San Bernardino National Forest (SBNF) with participants from the University of California at Riverside and Berkeley; the USDA, Forest Service and the Pacific Southwest Forest and Range Experiment Station, Riverside, California. This study was funded principally by the U.S. Environmental Protection Agency (EPA) through the Environmental Research Laboratory in Corvallis, Oregon. The research team investigated two questions: 1) How do the organisms and biological processes of the conifer forest respond to different levels of chronic oxidant exposure? and 2) How can these responses be interpreted within an ecosystem context?

Due to preexisting damage by air pollution, the SBNF project was constrained to observe up to 30 years of accumulated effects on populations and processes at selected research plots along a gradient of decreasing ozone stress (Figure 1). The ozone stress gradient was

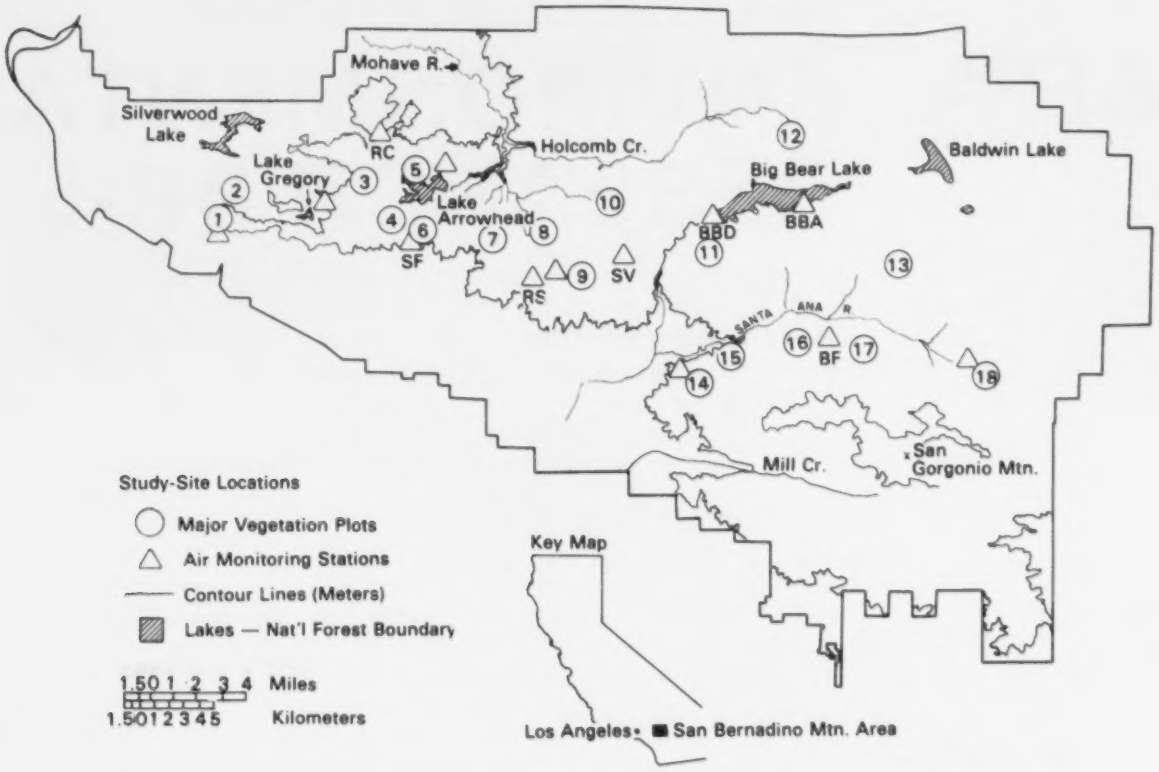


Figure 1. Location of major study sites in the San Bernardio National Forest.

paralleled by a gradient of decreasing precipitation and air temperature (with increasing altitude). Consequently, as precipitation and air temperature decreased, the most common conifer species forming the matrix of the forest mixtures shifted from ponderosa pine *(Pinus ponderosa* Laws) to Jeffrey pine *(P. jeffreyi* Grev. and Balf.). It was not possible to locate a suitable ponderosa pine stand free from ozone stress in southern California that could be used as a control in the study. The topography, geology, soils, climate, and vegetation of the San Bernardino Mountains have been described in earlier reports.[4-7]

One independent research group used some of the study sites for a survey of the diversity and health of the lichen flora.[8] A second group completed an intensive study of photosynthesis and transpiration of ponderosa pine experiencing severe chronic ozone exposure.[9]

Data Collection and Management

The data collection methods used by individual investigators have been described in progress reports.[7,10] Most of this research focused on 18 permanent plots during the summers of 1972 through 1978 (Figure 1). Some investigators found it necessary to limit their studies to particular plots, or to establish additional temporary plots in order to obtain a forest-wide perspective of vegetation recovery after fire[11] and the activity of insects and diseases responsible for tree mortality.[12]

The data base of the entire project was centralized.[10] All data sets, including up to 200 data types, were stored on the operating system disk of an IBM 370/145, where they were available for transfer to a mini-disk in the interactive environment of the computer. Studies by the separate teams provided data on: 1) air temperature, relative humidity, precipitation and transpiration regimes; 2) water availability as a function of soil and site attributes; 3) concentration of ozone in the study area; 4) foliage injury along the gradient of ozone dose; 5) leaf litter fall; 6) decay of litter and partitioning of selected nutrients; 7) tree seed production; 8) seedling establishment; 9) tree growth; 10) insect and disease complexes responsible for tree mortality; and 11) fire history in relation to stand species and age composition.

For purposes of analysis in an ecological systems analysis context, the physical and biological components of the ecosystem, and four essential ecosystem processes were defined as follows. The major physical components are water (precipitation), temperature, light, mineral nutrients (soil substrate), and ozone air pollution. Biological components include the producers represented by an assortment of tree species and lichens; the consumers or wildlife that consume tree seeds and young seedlings, and insect and disease organisms causing tree mortality; and the decomposers, principally the populations of saprophytic fungi particularly responsible for leaf and woody litter decay.

The major ecosystem processes represented are: 1) the flow of carbon from the atmosphere to be incorporated initially into green plant biomass, and then partitioned among consumers, litter and decomposer mass, the soil and back to the atmosphere; 2) the flow of water in the soil-plant-atmosphere continuum; 3) the flow of mineral nutrients through the green plant, litter, and soil-water compartments; and 4) the shift of diversity patterns in time and space as represented mainly by changes in tree stand species composition, age, structure, and tree density.

Results

Temporal Variation of Ozone Dose, Temperature, and Precipitation

Ozone dose, temperature, and precipitation trends during the study period were critical because these variables drive the ecosystem processes (Figure 2). During the 1973 through 1978 term of the project, the May through September ozone dose at Sky Forest indicated a definite downtrend until 1978, when dose increased again.[13] This trend is more closely correlated with meteorological variation from year-to-year than with changes in amounts of ozone precursors, according to another study of South Coast Air Basin trends.[14] The May through September average hourly air temperature ranged between 14.7 and 17.0°C during the five-year data collection period. The mean temperature for the five years was 15.6 ± 1.0°C. The highest average air temperature occurred in 1975, the year of lowest annual precipitation. The precipitation at nearby Lake Arrowhead (3 km north of Sky Forest) was below the 30-year average of 1055 mm during the first four precipitation years and considerably above average during the last year. However, the monthly distribution of precipitation is more important than the annual total because it determines the water available to plants during the growing season.[15] Higher-than-average precipitation during the late spring, late summer, and early fall is much more favorable for vegetation growth and other ecosystem processes that are moisture limited. During 1975-76, 1976-77, and 1977-78, there were unusually large amounts of precipitation in August and September. This is a marked departure from the long-term average for late summer months. This deviation has important implications for interpretation of the entire study results because the expected late summer drought did not occur during three consecutive years. These annual trends of ozone dose, temperature, and precipitation at Sky Forest-Lake Arrowhead are considered representative of the entire study area, after adjustments for distance and elevations.[13]

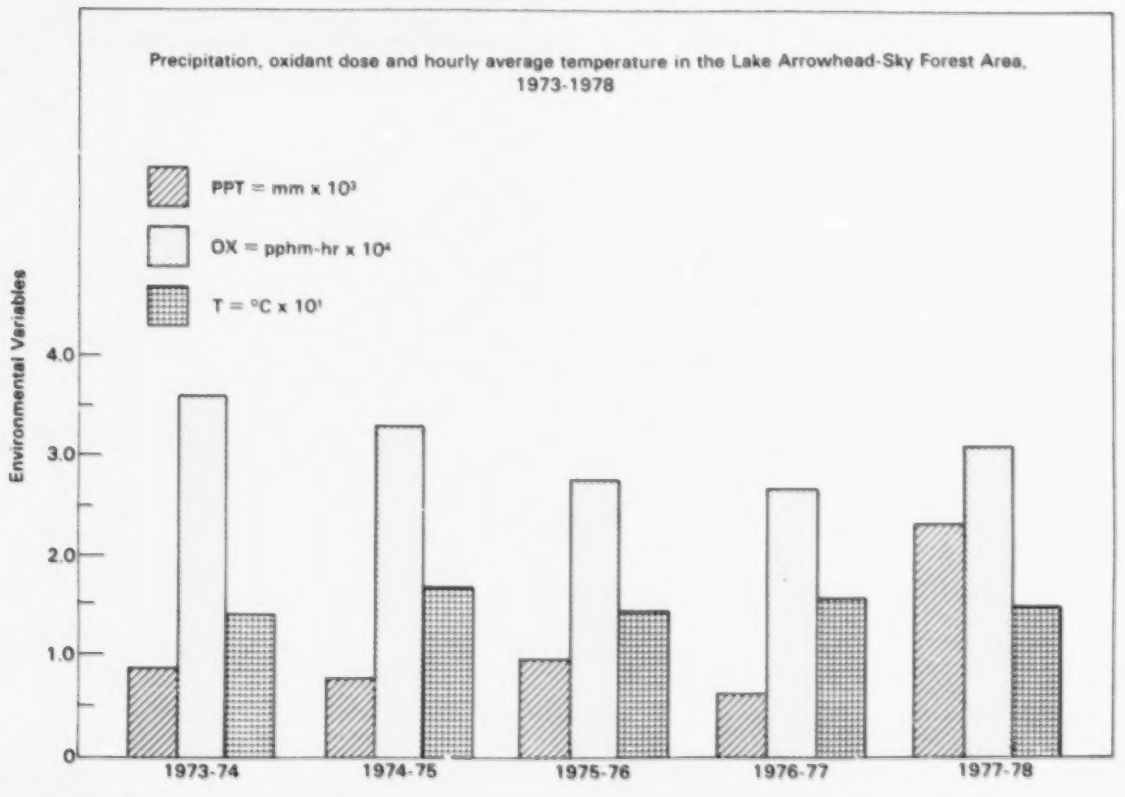


Figure 2. Annual trends of ozone dose precipitation and air temperature near the Lake Arrowhead-Sky Forest region of the San Bernardino National Forest.

Spatial Variation of Ozone Dose

Oxidant monitoring stations (Figure 3) along the major west-to-east axis of pollution transport extending for 50 km at elevations between 1500 and 2300 m showed that between 30 to 45 km, where the May-September hourly average ozone concentration ranged from 5-6 pphm, chronic damage to ponderosa and Jeffrey pine was barely detectable. The injury threshold between 30 and 45 km was highly influenced by terrain features. Beyond 45 km, the natural background ozone concentration was 3-4 pphm, comparable to other mountain areas in the United States. The daylight ozone dose at a mountain station located at 12 km along the 50-km transport axis was 40% higher than the nearest urban station which was located 1349 m lower and 15 km to the southwest. This large difference is due to the processes supporting the nocturnal preservation of ozone at higher elevations.

Effects of Chronic Ozone Stress on Ecosystem Processes

Carbon Flow

During a highly instrumented study at a single plot, a research team from Lawrence Livermore National Laboratory (LLNL) found that the photosynthetic rate of the needles of ponderosa pines classed as having slight, moderate, or severe chronic injury was reduced to about 10% of the maximum observed rate after experiencing 800, 700, and 450 pphm ozone, respectively.[9] Stressed trees also retained a smaller amount of assimilated carbon after respiration losses.

Three years of parallel observations of ponderosa and Jeffrey pines at five sites ranging from low to high ozone environments provided dose-injury relationships based on the increase of visible needle symptoms and needle abscission rates.[16] The largest increments of needle symptom increase occurred in the early summer; needle abscission started during the second year of exposure and the largest numbers of needles were lost during the winter. The most important variable governing dose response was the inherent level of tree sensitivity to ozone which was defined by the average number of annual needle whorls retained by each tree.

The changes in the number of annual needle whorls retained by 951 ponderosa and 769 Jeffrey pines distributed throughout the 18 study plots indicate a decrease from 2.5 to 2.0 whorls from 1973-1978 at 12 plots experiencing hourly average ozone concentrations ranging from 6-12 pphm.[17] Pines at the six plots with lower doses maintained the same number of whorls or showed a slight increase.

The proportion of needle whorls retained which had slight to severe ozone injury symptoms, varied from year to year.[17] In 1975, there was a sudden decline of injured foliage retained by trees experiencing 6-12 pphm ozone. This peak of needle abscission followed the highest seasonal ozone dose of the period, which occurred in 1974,

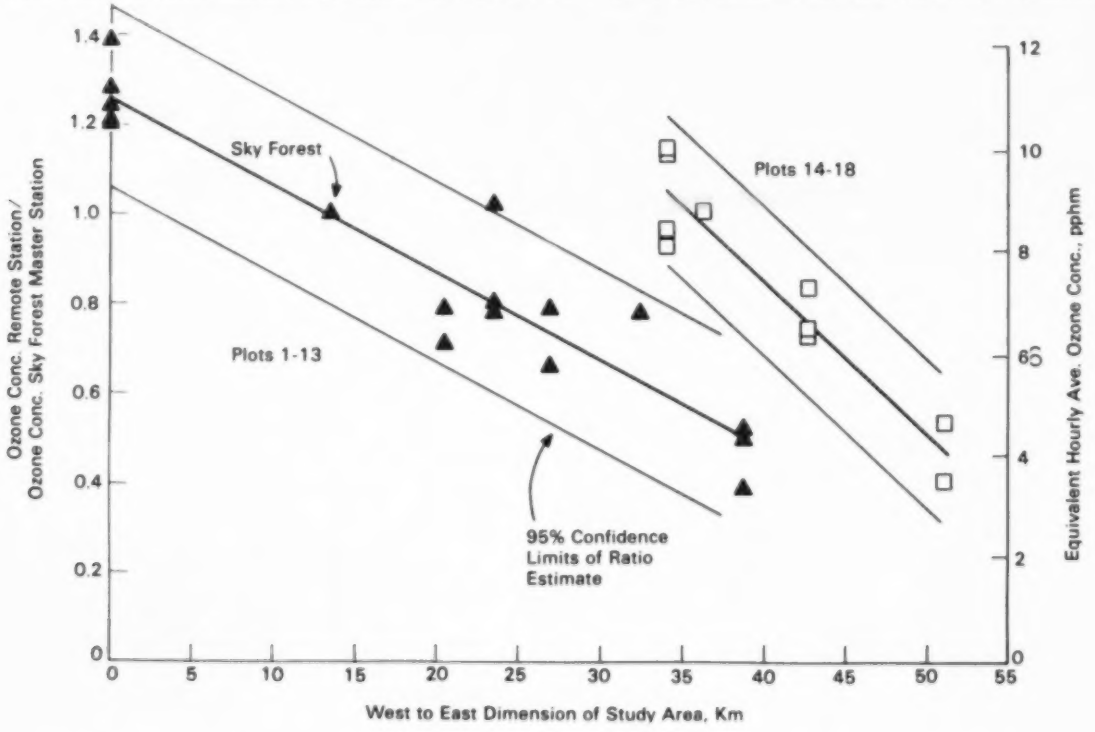


Figure 3. The estimated gradients of ozone concentration along two west to east axes representing the major terrain-influenced transport patterns.

and was coincident with highest summer temperature and one of the lowest precipitation amounts for the 1973-78 period. The average number of annual needle whorls retained by 502 white fir remained about the same during the 1973-78 period but at all dose levels the proportion of injured needle whorls decreased and uninjured whorls increased.[17]

The 378 California black oaks in the study plots showed a sensitive leaf injury response to ozone each year,[18] but the 97 incense cedars and 68 sugar pines were generally slow to show ozone injury.[18] Measurements of the difference of diameter-at-breast-height (dbh) between 1975 and 1978 for 951 ponderosa and 769 Jeffrey pines showed moderate correlation with number of annual needle whorls retained (a range of 1-7 whorls). The correlation was closer for the 10-29.9 cm dbh trees than for the trees 30 cm dbh and larger.[19]

Tree ring analysis to investigate the variations in annual ring growth was approached cautiously because, as a result of ozone or drought stress, many trees failed to produce a ring.[20] For those trees which fit the master ring chronology for the part of the study area in question, the model which best characterized ring growth was a negative exponential curve.[21] The degree of deviation from this model could be explained by the variability in ring growth during the 1950-75 period. The logarithm of winter precipitation and autocorrelation with the previous years' growth were the strongest variables predicting growth of trees at plots experiencing no pollutant effect; at the high ozone dose plots the correlation was much lower for these variables. The positive relationship between needle whorl retention and ring width was also significant. The effects of temperature were ambiguous.[21]

Measurements of ponderosa pine stem growth by change in dbh and ring analysis both showed that surviving trees at high-dose plots demonstrated sudden growth increases 1) due to thinning resulting from death of sensitive trees or salvage logging to remove weakened trees[19,21] and 2) as a result of reduced competition from surrounding trees. Both annual ring and stem diameter difference measurements[22] showed radial growth reductions for sensitive blackout[22] and white fir.[19,21]

Cone production in both injured and uninjured ponderosa and Jeffrey pine stands was mostly influenced by crown class or the position of the tree's crown relative to its neighbors. Dominant ponderosa pine comprised 32 percent of the trees and produced 80 percent of the cones. Cone production also increased with age. However, injured ponderosa and Jeffrey pines older than 130 years produced significantly fewer cones per tree than uninjured trees of the same age.[23] Severe injury to both dominant and codominant ponderosa and Jeffrey pines resulted in fewer cone crops during the six years of study. The drop in proportion of trees in severe injury classes that produced cones was much more dramatic for Jeffrey pine than for ponderosa. Tree ring analysis showed a positive and significant relationship between cone production and radial growth.

Nutrient Flow

The largest amount of needle litter, an average of 357 g/m^2, was found under ponderosa pines moderately damaged by ozone. There was 90 g/m^2 of litter under severely damaged trees and 131 g/m^2 under healthy trees.[24] The negative effects of heavy accumulations include an increased fuel load and the hinderance of successful pine seedling establishment. In the event of fires, the large nutrient store in a thick needle litter layer would be lost by volatilization and subsequent surface runoff. The benefits of heavy litter include significant increases in surface soil carbon, nitrogen, the carbon/nitrogen ratio, and exchangeable calcium. Lower absolute amounts of N, P, K, Ca, and Mg were found in the living foliage of injured ponderosa pines. Back translocation of all five elements and also dry matter from leaves is curtailed, indicating an interference in the tree's internal conservation of nutrients.[25] Nitrogen, calcium, and magnesium concentrations in throughfall are higher under injured trees.[26]

The decomposition of litter comprised of ozone-injured needles was more rapid; it was inversely correlated with solar radiation and positively correlated with litter depth. Moisture was the single most important variable limiting decomposition;[27] nitrogen and phosphorus did not affect the process.

The taxonomic richness and population density of fungi which colonize living needles and later participate in decomposition were both reduced by ozone injury because the normal increase with age was prevented by premature needle senescence and abscission. This change could weaken the functional stability of the decomposer community.[27]

Moisture Flow

Ponderosa pine crowns intercepted 19.0, 22.4, and 21.6 mm of rain at 1, 2, and 3 m, respectively, from the stem, compared to 19.4 mm for a nearby clearing. As leaf surface area is decreased by oxidant injury, rain throughfall increases until it is nearly the same as precipitation amounts in clearings.[26] This implies that fog condensation would also increase under injured trees. Consequently, litter moisture could be expected to evaporate more rapidly since thinner crowns would also allow more radiation to reach the litter surface.

The summer season flux of moisture in the soil-plant-atmosphere continuum was investigated by weekly measurements of available soil moisture at several depths down to 274 cm[15] and biweekly measurements of pre-dawn twig xylem water potential.[16] Trees continued to obtain moisture from lower depths when moisture in the top 274 cm was depleted. A transpiration simulation model provided corroborative evidence for the summer water use pattern and suggested that higher transpiration rate during early summer months may be partially responsible for the large incremental increases of ozone injury to needles observed in June and early July.[16]

An ozone-induced decline of stomatal conductance was observed by the LLNL research group after the early summer ozone exposure. This observation and the fact that leaf surface area is much lower for the ozone-sensitive genotypes implies lower transpiration losses for stands containing many sensitive or moderately sensitive trees.[9,28] Diminished competition for water in such stands is undoubtedly related to the sudden growth improvement of the more ozone-tolerant genotypes that was detected with tree ring analysis.[21]

Shift of Diversity in Time and Space

The preexisting species mixture in the SBNF conifer zone includes five types: 1) ponderosa pine; 2) ponderosa pine-white fir; 3) ponderosa pine-Jeffrey pine; 4) Jeffrey pine-white fir; and 4) Jeffrey pine. The stands most subject to ozone damage are those containing ponderosa pine. The changes in species and age composition after long-term exposure to ozone were considered the most important measures of oxidant impact because these qualities have greatest implications for human welfare. The effects of air pollution are superimposed on natural variables which interact to control species establishment and survival, e.g., moisture availability and suitable space, fire frequency and intensity, and mortality caused by various diseases and insects.[20,21]

Two distinct patterns of successional development were recognized in the study area,[11] namely autogenic and allogenic succession. With autogenic succesion, changes in the forest environment caused by existing trees promote continuous establishment of species more tolerant to lower light intensity in the understory. This process is taking place on sites not recently disturbed by fire, diseases, or insects. In stands affected by significant ozone damage, pine needle litter accumulation and a heavy layer of combustible litter accumulation following pine mortality combined with the development of a living fuel ladder created by the shade and oxidant-tolerant species in the understory will lead to crown fires that could eliminate the entire tree layer. There would be few surviving pines to provide the seed required to reestablish the pine overstory.[29] Even without a catastrophic fire event, pine establishment is limited by the lower seed production of injured trees and the thick litter layer that contributes to fungal infection and death of germinating seeds.

Air pollution-injured overstory pines are more readily killed by *Fomes annosus* root disease[30,31] because the fungus colonizes freshly cut stump surfaces of weakened trees more rapidly, thus speeding up the spread rate from stumps to nearby living roots. The fungus spreads more rapidly in the roots of weakened trees than in healthy trees. Fewer western pine beetles *(Dendroctonus brevicomis)* are required to kill weakened trees; therefore, in stands with many weakened trees, a given population of western pine beetles could kill more trees and increase at a faster rate.[32] *Fomes annosus* and the western pine beetle are often present in the same tree. The continuous effects of ozone during the years of low moisture stress results in the accumulation of weakened trees; therefore, mortality rates from diseases and insects peaked during years when soil moisture was limited.

Three ring analysis showed that the period of decreasing vigor in the 5-10 year period preceding tree death correlated with tree age, i.e., more younger trees died during the period of observation than older trees.

The probable elimination of autogenic succession at many sites following inevitable crown fires is expected to cause a shift to allogenic succession where changes in plant communities result from environmental modifications (repeated fires) not caused by the plants themselves.[29] Tree and shrub species adapted to survive fire by sprouting from the stem or root crown dominate this vegetation cover. In the San Bernardino National Forest, there are already vast acreages converted to various mixtures of oaks and shrubs. These areas range from impenetrable brush to oak woodlands, which in most cases are self-perpetuating because rapid crown closure creates an unfavorable environment for the return of conifer species, and after each fire these species resprout.[11]

Black oak is an important species in this vegetation mixture. The crowns of this deciduous oak provides favorable understory conditions for the best conditions for the reestablishment of conifers, particularly ponderosa pine. Black oak is slightly to moderately sensitive to ozone, but this degree of sensitivity should not seriously disrupt its "nurse tree" role with respect to ponderosa pine.

Discussion

The essential interactions of physical ecosystem components and four ecosystem processes, namely the flows of carbon,

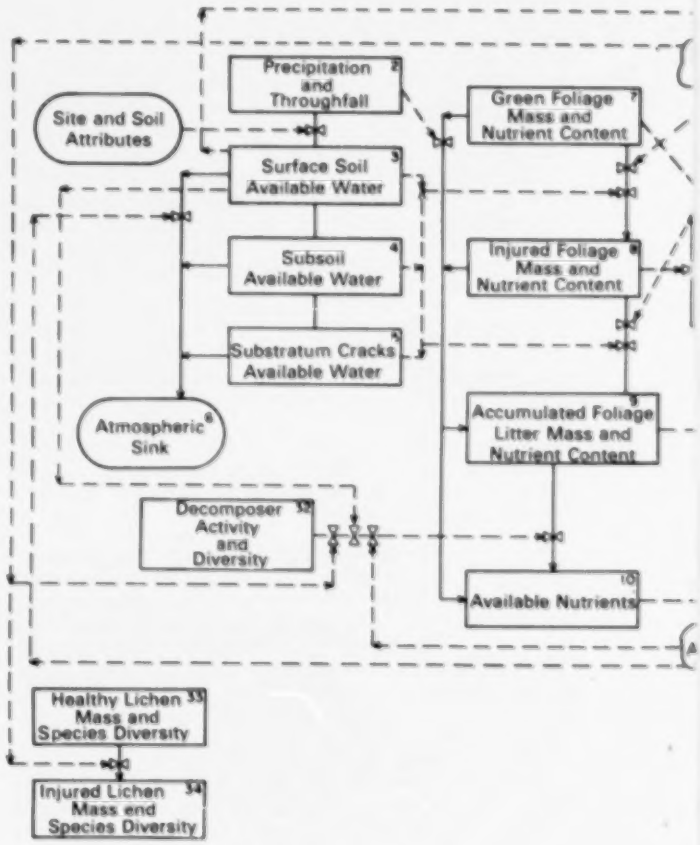
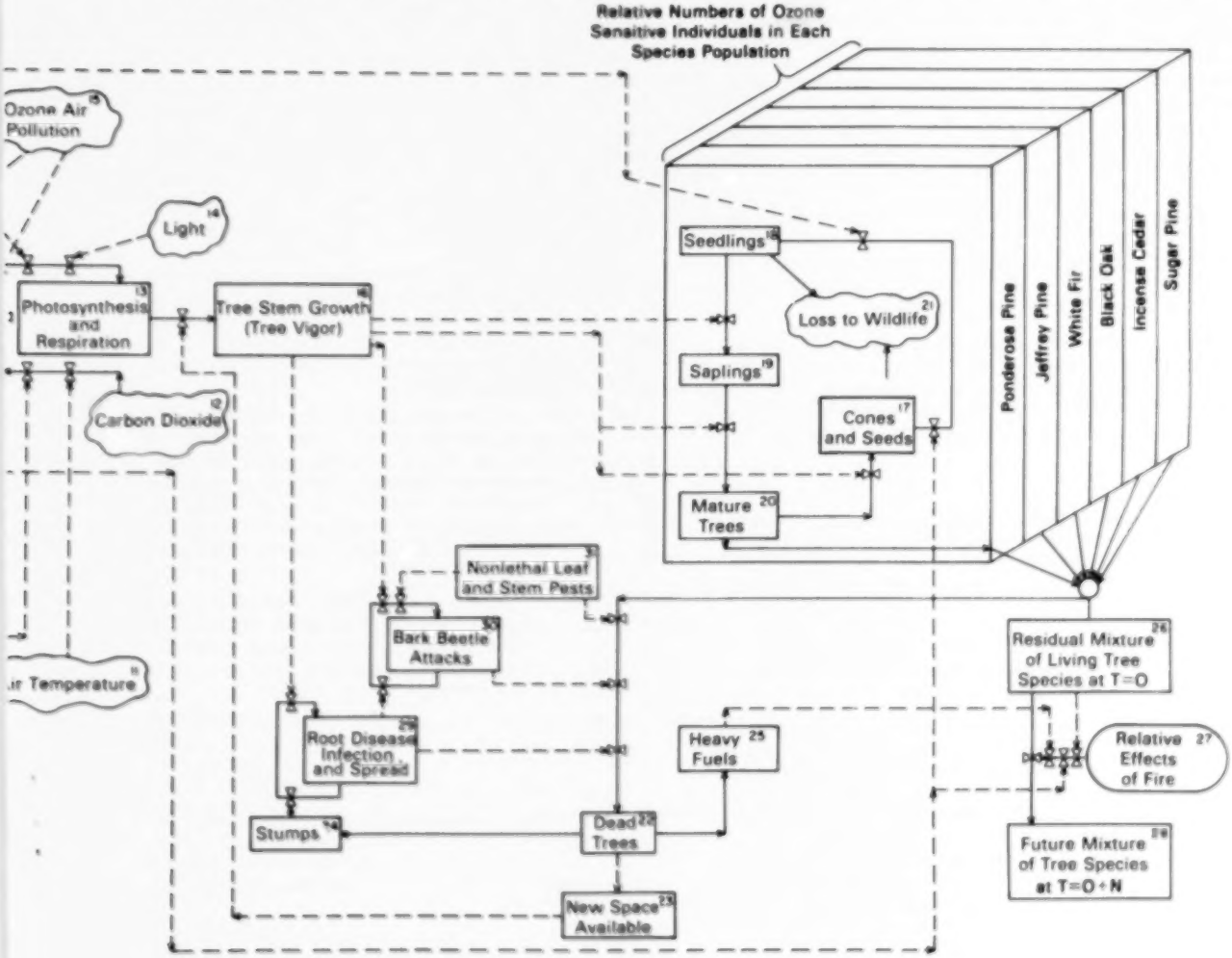

Precipitation and Throughfall 2
Site and Soil Attributes
Surface Soil Available Water 3
Subsoil Available Water 4
Substratum Cracks Available Water
Atmospheric Sink 6
Green Foliage Mass and Nutrient Content 7
Injured Foliage Mass and Nutrient Content 8
Accumulated Foliage Litter Mass and Nutrient Content 9
Decomposer Activity and Diversity 12
Available Nutrients 10
Healthy Lichen Mass and Species Diversity 33
Injured Lichen Mass and Species Diversity 34

Figure 4. Diagrammatic model of the effects of chronic ozone air pollution

nutrients, and water, and the shift of diversity patterns in time and space, are summarized in Figure 4. This scheme also suggests the submodels that will be required for future development of simulation modeling.

Solid lines connecting boxes indicate material flow from compartment to compartment. Dashed lines indicate the controlling influence of one variable on the flow between compartments. The controlling "valve" resembles a bow tie.

Compartments (2 through 6) represent the flow of water in the soil-plant-atmosphere continuum which is modified by several site, soil, and geologic substratum attributes. Water availability (2 through 5) influences the flux of ozone (15) to both healthy and injured foliage and therefore exercises control on foliage injury, abscission, and litter accumulation (7 through 9). The flow of nutrients to the litter layer (also 7 through 9) is influenced by leaching due to precipitation contracting foliage during throughfall (2) as well as the rate of needle fall to the litter surface (9). The relative amounts of healthy (7) and injured foliage (8) remaining in the crowns have a direct effect on carbon assimulation and carbon loss (13) and finally the growth of trees of all size classes (16, 18, 19). Photosynthesis is further controlled by available nutrients (10), air temperature (11), carbon dioxide concentration in the atmosphere (12), and light availability as influenced mainly by tree density. Decomposer activity and diversity (32) is only indirectly affected by ozone (15); however, air temperature (11) and particularly surface soil-available water (3) control the rate of litter decomposition and availability of nutrients (10). The processes of seed production, seedling establishment, and reactions to competition as different species grow through several size classes are indicated in compartments 17 through 20. These processes for different species will be decreasingly influenced by ozone effects in the following order:



stress on a western coniferous forest ecosystem.

ponderosa and Jeffrey pine, white fir, black oak, incense cedar, and sugar pine. The establishment of the more ozone sensitive species (particularly ponderosa pine) will be influenced by diminished seed production (17) and losses to wildlife, mainly tree squirrels (21). Surface soil-available water (3) exercises the most important control over the survival of seedlings (18). Tree mortality rates are closely related to the number of ozone-sensitive individuals in each species population (20). The low vigor of ozone-injured trees (16) encourages the interactions of the insect and disease complex (29, 30, 31) resulting in tree mortality (22) and alteration of the stand environment by making new space available (23). The reduction of competition among the remaining trees leads to a growth release for ozone-tolerant genotypes. The continuing effects of ozone (15) and the pest complex (29, 30, and 31) result in accumulation of stumps which encourages the *Fomes annosus* root disease cycle (24, 29). Additional amounts of leaf litter (9) and a heavy layer of combustible litter (25) have the effect of increasing the fire hazard (27) to the residual mixture of tree species (26), particularly since ozone-tolerant, fire-sensitive understory trees can form a living fuel ladder that carries the fire to the crowns of the fire-tolerant overstory trees. Where crown fires are prevented, the future mixture of tree species (28) may be dominated by allogenic succession which will reestablish the desirable ponderosa- or Jeffrey pine-dominated forest. If crown fires are not prevented, the autogenic successional process will dominate and the oak species and less desirable shrubs that sprout after fire will be perpetuated as the vegetation cover. Only black oak is ozone-sensitive. Foliose lichen mass and diversity change (33, 34) provide another example of the direct impact of ozone.

The effects of chronic ozone stress on this web of interactions will vary considerably with ozone concentrations and other physical and biological factors. Predictive capability will improve with additional experimentation using the existing data base and computer simulation models.

Conclusions

1. For the five year period of this study, average 24-hour ozone concentrations in the San Bernardino Mountains during the May through September period ranged from a background of 3-4 pphm up to maxima in the range of 10-12 pphm.

2. The first evidences of ozone injury to sensitive ponderosa and Jeffrey pines were observed at 24-hour averages in the range of 5-6 pphm.

3. Occurrence of high nocturnal ozone concentrations at mountain sites, compared to basin sites as reported elsewhere, was confirmed for the San Bernardino Mountain area. Here, a mountain station received a daylight-hour dose 40% higher than a nearby basin station that was 1378 m lower in elevation, mainly because higher nocturnal concentrations were still being seen in the early morning and late evening (3 hours following sunrise and preceding sunset).

4. Ecosystem components most directly affected by ozone were tree species, the fungal microflora of needle leaves, and foliose lichens occupying tree bark.

5. The most important ecosystem processes affected either directly or indirectly were flows of carbon, mineral nutrients and water, and changes in patterns of vegetation cover diversity over time and in space.

6. The diminished flow of carbon in the tree layer of the ecosystem was associated with diminished foliage surface of affected trees and decreased photosynthetic capacity of the remaining foliage.

7. Diminished photosynthetic capacity resulted in decreased stem diameter and height growth and reduced seed production in the injured ponderosa and Jeffrey pines.

8. The store of carbon and mineral nutrients accumulated in the thick needle litter layer under stands of ozone-injured trees influenced nutrient availability due to losses by volatilization during fires and in subsequent surface runoff; the mere increase of litter thickness inhibits pine seedling establishment. Without fire, the surface soil may be more enriched by carbon and mineral nutrients from excessive litter.

9. The last three consecutive summers of data collection (1976 to 1978) were atypical because unseasonal rainfall prevented the usual late summer drought stress. Injured foliage did not drop as readily, there were significant stem diameter growth differences between 1975 and 1978, and tree mortality rates declined. These conditions might not have occurred during the typical late summer drought.

10. The large proportion of missing rings in ozone-stressed areas confounded attempts to use tree ring analysis to fit study trees to a master ring chronology for each of several distinct regions. The model which best characterized tree ring growth of the past 30 years was a negative exponential curve.

11. Interception of rain and fog by the forest canopy increased precipitation under trees compared to clearings. The thinning of needles associated with injured pines allowed increased amounts of moisture to fall to the forest floor. These high moisture conditions and the increased radiation that reaches the litter surface may influence litter decomposition and tree seedling establishment.

12. The biweekly incremental increases of ozone injury to needles of ponderosa and Jeffrey pines were larger during the early season period of high moisture availability and high transpiration, but a causal relationship was not established.

13. *Fomes annosus* root disease can be expected to increase more rapidly in ozone-injured pine stands because freshly cut stumps and roots of weakened trees are more vulnerable to fungus attacks.

14. Fewer western pine beetles *(Dendroctonus brevicomis)* are required to kill weak pines. In stands with a high proportion of ozone-injured trees, a given population of western pine beetles could kill more trees and increase at a greater rate.

15. Forest stand age and species structure are variables that have the most relevance and direct effect on human welfare in both recreational and commercial forests. The interplay of insects and diseases, drought, ozone

injury, and forest fires shapes stand age and species structure. Forest management practices can alter these factors significantly.

16. In the absence of fire, the gradual destruction of ponderosa or Jeffrey pine overstory by ozone and other agents has lead to an accumulation of heavy woody fuels and an understory of ozone-tolerant, fire-sensitive species that form a living fuel ladder, likely leading to crown fires which will consume the remaining pines. In devastating fires, there would be total loss of forest cover, requiring expensive reforestation. Without the pine-dominated forest, a less desirable cover of shrub and oak species emerges as a self-perpetuating community of species that sprout after fire, quickly obtain crown closure, and inhibit the natural reestablishment of pines and other conifers.

Recommendations

Air quality control measures that manage to maintain summer season, 24-hour ozone concentration averages below 5-6 pphm in the forested receptor areas of California are required to prevent injury to sensitive species and to prevent initiating undesirable changes in carbon, water and mineral nutrient flows, and patterns of diversity in time and space.

In circumstances where air quality cannot be maintained below the 5-6 pphm average, there are still significant opportunities to ameliorate adverse effects with known, operational forest management practices. Additional work is needed to refine these management prescriptions.

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